COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XII
PRELIMINARY OBSERVATIONS UPON THE STRUCTURE OF THE EPIDERMIS, STOMATA, AND CUTICLE

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THE TAXONOMIC SIGNIFICANCE OF structural variations in stomatal apparatuses [2] was strongly emphasized by Solereder (1899). Following the earlier work of Prantl (1872), Vesque (1889) and others, he distinguished a number of significant structural types, e.g., rubiaceous, false rubiaceous, cruciferous, caryophylleous. In the rubiaceous types (paracytic forms of Metcalfe and Chalk, 1950) the stomata are accompanied on either side by one or more accessory cells oriented parallel to the long axis of the pore and guard cells. In the true rubiaceous type the subsidiary cells are derived from the same mother cell as the guard cells; whereas in the false rubiaceous forms the accessory cells arise by secondary divisions in neighboring epidermal cells. Since the publication of Strasburger's (1866–67) paper, the Cactaceae have been regarded by later investigators as having stomatal apparatuses of the true rubiaceous form.

In securing stems of varying sizes and ages preserved in formalin-acetic-alcohol (as a basis for investigations of the xylem reported upon in preceding papers of this series), younger stems bearing leaves were usually included in collections of *Pereskia, Pereskiopsis* and *Quiabentia*. Such collections are difficult to obtain and have involved the active cooperation of many botanists. Young stems and leaves being thus available, it seemed advisable to initiate preliminary investigations, not only of stomata, but also of the epidermis and cuticle.

The leaves of the three genera now available to me commonly have two, three, or four thin walled, crescent shaped subsidiary cells oriented parallel to the guard cells of the stomata (FIGS. 1–4). At times there is but one subsidiary cell and at others secondary transverse divisions may occur in one or more of the subsidiary cells. Infrequently, in aberrant leaves some of the stomata appear to have no accessory cells derived from the same mother cell as the guard cells.

The thin walled, crescent shaped accessory cells appear at least superficially to be derived from the same mother cell as the guard cells, in conformity with Strasburger's conclusion based upon detailed developmental

[2] In this paper stoma and stomata are used in referring to a pair of guard cells and the aperture between them, stomatal apparatus where subsidiary or accessory cells are involved in addition.

investigations of stomata in *Pereskia aculeata* Mill. and other cacti. Such an interpretation is strengthened by the not infrequent occurrence of groups of four or more thin walled, slender cells oriented parallel to each other, but not having completed differentiation of guard cells and an aperture between them.

As seen in surface views, the size and number of the stomata and the number and transverse diameter of the crescent shaped subsidiary cells varies more or less markedly in different leaves of the same taxon, in different leaves of the same plant, and in different parts of the same leaf. Similar forms of stomatal apparatuses occur in the epidermis of young stems.

The size, form, and orientation of epidermal cells is highly variable in the three genera. At times the anticlinal walls of the cells are smooth (FIGS. 2 and 4), whereas in other cases they are conspicuously undulating (FIG. 3). The stomatal apparatus may be jacketed by epidermal cells of but slightly modified size and form (FIG. 3). They may be completely (FIG. 1+), or partly (FIG. 4) jacketed by a pair of epidermal cells whose longer curved axis is oriented parallel to that of the guard cells and subsidiary cells. One or both of these curved epidermal cells may have secondary transverse divisions (FIG. 2). Where the pair of epidermal cells does not completely jacket the stomatal apparatus, one, two or more conspicuously small epidermal cells oriented at right angles to the major axis of the guard cells may be present (FIG. 4+). In some cases the stomatal apparatus tends to be jacketed by a ring of small epidermal cells. In other cases the stomatal apparatus is situated in a broadened complex of small epidermal cells (FIG. 12).

Owing to variations in the breadth of subsidiary cells and their tendency to divide transversely at times, and to variations in the size, form, and orientation of epidermal cells which jacket the stomatal apparatuses, it is difficult in some cases — without developmental evidence — to determine with certainty which accessory cells arise from the same mother cell as the guard cells. Furthermore, owing to the wide ranges of structural variability of the epidermis and stomatal apparatuses within a taxon, morphological criteria for differentiating taxa are of uncertain reliability unless based upon very extensive collections of leaves and young stems from plants of different ages when grown under varying environmental influences. However, the cuticle, epidermis, stomata, and sub-epidermal layers of available material, when studied in adequately stained periclinal and anticlinal sections, appear to provide potentially useful criteria in the comparison of different categories of *Pereskia*, and in distinguishing the genus from *Pereskiopsis* and *Quiabentia*. In addition, such investigations are particularly desirable from a physiological point of view in regard to the structure and functioning of stomata, and in studying the conservation of moisture in leaves and in young stems prior to periderm formation.

As shown in the second paper of this series (Bailey, 1961a), *Pereskia sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., *P. moorei* Britt. & Rose, *P. tampicana* Web. and *P. corrugata* Cutak belong in a distinct

category of pereskias characterized by having consistently occurring forms of aggregated fiber-sclereids in their secondary phloem. Their xylem exhibits less divergent trends of specialization than that of other pereskias (Bailey, 1962, 1963c). In this category of taxa, having large, thin, pinnately veined leaves, stomata are at times few in number or absent on the upper or adaxial surface of the foliar appendages.

When epidermal peels are stained in sudan III or in sudan III and Haidenhein's haematoxylin and mounted in glycerin, the cuticle and the outer periclinal wall of the epidermal cells either exhibit no conspicuous structural patterns (FIG. 1), or have variously oriented striations (FIG. 5). In view of the emphasis that has been placed upon cuticular striations in taxonomic investigations it is essential to determine whether such striations are present in unmodified living leaves or are produced by differential contractions of the cuticle and epidermal walls during fixation, dehydration, and other treatments. In the pereskias discussed in the preceding paragraph, cuticular striations, when present, are not due primarily to inequalities in thickness of the cuticle but to contractions of a cuticle of relatively uniform thickness forming folds or ridges. It is significant in this connection that in unlignified, unsuberized and uncutinized meristematic and other tissues of plants the primary walls contract markedly during dehydration. Furthermore, adjacent tissues in intact plants not infrequently are under differential tensions which may be released or modified in peels or sections of leaves producing morphological changes even prior to dehydration. Where cuticular striations occur, the primary walls of the epidermal cells are smooth except for the outer surface of the outermost walls which have projections or ridges corresponding to the folds in the cuticle.

In *Pereskia sacharosa* and allied taxa the cuticular striations, when present, vary markedly in form and orientation, not only in different leaves of the same taxon or plant, but also in different parts of a single leaf. At times, they may be linear and parallel to one another and may extend from cell to cell particularly in axially elongated cells overlying the midvein. They may be radially oriented in relation to the stomata or some particular cell of the epidermis (FIG. 5). In other cases they may be variously convoluted and oriented. The variations in pattern appear to be correlated with variations in the size, form, and orientation of the epidermal cells and to the thickness and degree of contraction of primary walls during dehydration. The range of variability is so extensive as to render difficult and laborious any attempt to differentiate species upon the basis of such diagnostic criteria. It should not be inferred from this, however, that even where cuticular striations are induced by dehydration in other families, differences in the presence or absence of such structures may not be due to consistent differences in the cellular structure and behavior of the leaves in related species.

In the leaves of the category of pereskias under discussion, the outer cells of the mesophyll are relatively large and thin walled (FIG. 7). The stomata are subtended by intercellular spaces of irregular ramifying form

in the chlorenchymatous tissue. As seen in median sectional view, the more or less circular guard cells have thickened walls on their upper and lower surfaces. The first pair of subsidiary cells are thin walled and their internal extensions curve about the guard cells exhibiting various degrees of approximation. The relatively thin part of the cuticle overlying the stomatal apparatus curves inwardly into the frontal cavity forming slender outer "ledges" but commonly more slender than those illustrated in FIG. 15. Very tenuous extensions of the cuticle pass inwardly lining surfaces of the aperture but without forming conspicuous internal ledges as in some dicotyledonous plants. Inner extensions of the tenuous cuticle may likewise occur on the exposed surfaces of cells in the subtending intercellular cavity of the mesophyll.[3] It appears likely that in the above category of stomatal apparatuses closure of the stomata may result (1) by contact between the outer cuticular ledges, (2) by contact between the guard cells, and (3) by approximation of the inner parts of the first-formed pair of subsidiary cells, as in (FIG. 7).

In vigorous, rapidly elongating shoots, periderm formation is retarded; in the case of internodes, appearing first in parts at a considerable distance below the apex of a stem. The lower internodes have a markedly thickened cuticle and massive, wedge shaped accumulations of cutin which extend inward between the epidermal cells (FIG. 16).[4] Although the cells of the outer cortex tend to be smaller, no collenchymatous outer layers or crystalliferous hypodermis are formed, as noted in the third paper of this series (Bailey, 1961b). Stomata are of sporadic and relatively infrequent occurrence, particularly in *P. sacharosa*, being absent in some internodes or parts of them. Where stomatal apparatuses are present, the walls of their cells are very thin (FIGS. 11 & 12), and the part of the cuticle which overlies them is tenuous. Furthermore, the cuticular ledges lining the entrance to the aperture are slender as in the case of leaves.

The genera *Pereskiopsis* and *Quiabentia* differ from this and other categories of *Pereskia* in having no characteristic forms of sclereids in their secondary phloem. In addition, the genera differ from this category of pereskias, in having highly advanced trends of divergent specialization in their xylem (Bailey, 1964). When epidermal peels of the comparatively thick, palmately or pseudo-palmately veined leaves are obtained, and are subjected to the same treatments and staining as those from the thin, pinnately veined leaves of the preceding pereskias, epidermal cells (with the exception of those of the stomatal apparatus) exhibit more or less conspicuous punctate or reticulate patterns of varying degrees of coarseness (FIGS. 2 & 4). At times cuticular striations are visible in addition. In anticlinal sections, these outer primary walls have a beaded appearance suggestive of inequalities in thickness. In surface views, the more intensive staining of parts of the reticulate patterns in haematoxylin suggests the

[3] For clarification of nomenclature and a general discussion of the structure of stomata see Esau (1953).

[4] From a strictly developmental, rather than a purely descriptive, point of view the thickening probably progresses largely from within outwardly.

possibility of differences in chemical composition. The structure of these walls obviously merits more detailed and comprehensive investigation since it may ultimately provide a significant criterion in differentiating leaves of *Pereskiopsis* and *Quiabentia* from those of *Pereskia*. All material available to me at present was preserved in F.A.A. It is essential to determine to what extent the reticulate patterns may have been induced or exaggerated by contractions due to dehydration as in the case of cuticular striations.

The leaves of *Pereskiopsis* and *Quiabentia* usually have abundant stomata on their upper as well as their lower surface. The cuticle overlying the epidermal cells tends to be of relatively uniform thickness except where it forms more or less massive accumulations above the central part of the guard cells and at times between the guard cells and subsidiary cells (compare FIGS. 17 & 18). These thicker parts of the cuticle deform the guard cells and depress them inwardly. In extreme cases, the central parts of the guard cells are greatly reduced in diameter (FIG. 18). This is in marked contrast to what occurs in the stomata of the pereskias discussed on preceding pages, where the cuticle merely forms slender ledges lining the entrance to the stomatal aperture.

These structural differences are strikingly demonstrated in anticlinal sections of young stems (FIGS. 17 & 18) which have numerous stomatal apparatuses, and in surface views of the epidermis when intensely stained in sudan III (FIG. 13). In the case of the pereskias, the thick cuticle forms massive intercellular intrusions between the cells of the epidermis except in the stomatal apparatuses (FIGS. 11 & 12). On the contrary, in young stems of *Pereskiopsis* and *Quiabentia* massive intrusions of the cuticle are largely confined to the stomatal apparatuses (FIG. 13).

It should be emphasized in these connections that it is essential in dealing with young stems to compare internodes in as nearly equivalent stages of development as possible, particularly those which have completed or nearly completed elongation prior to periderm formation. This is due to the fact that significant changes may occur in the cuticle, and in the cells of the epidermis and sub-epidermal layers during early stages of the elongation and increase in circumference of young stems. Similarly in dealing with leaves, changes in thickness of the cuticle, in the form of epidermal cells, and in the internal structure of stomata may occur during successive stages of the expansion and maturation of leaves. Furthermore, it should be kept in mind that unusually thin small leaves of shoots grown under certain environmental influences may vary more or less markedly in structure from larger thicker leaves of plants grown in different environments. This may account at least in part for the structural discrepancy between FIG. 3 (leaf from a rapidly elongating shoot in a greenhouse) and FIG. 6 (leaf from the slower growing branch of an old tree in its native habitat).

In sectional views of leaves and young stems of *Pereskia sacharosa* and allied taxa, the first pair of subsidiary cells commonly does not extend inwardly in excess of the general thickness of the epidermis (FIG. 7), whereas in the case of *Pereskiopsis* it is usually more extensive internally

(FIGS. 17 & 18). However, in both cases the innermost parts of the first pair of subsidiary cells exhibit varying degrees of approximation when not actually in contact, as in FIG. 7.

Young stems of *Perekiopsis* and *Quiabentia*, in contrast to those of the pereskias, are characterized by having collenchymatous layers and a well developed crystalliferous hypodermis subtending the epidermis (Bailey 1961b). This taxonomically and physiologically significant difference in structure is illustrated in FIGS. 14 & 19. Where collenchymatous layers are formed (FIG. 19) there are no intercellular spaces in the tissue except in clearly defined channels subtending the stomata. These channels communicate internally with intercellular spaces in the subtending, large, thin walled, chlorenchymatous tissue. They are jacketed by unpitted parts of the walls of collenchymatous cells (FIG. 22), and in turn by very tenuous intrusions of the cuticle, so tenuous as not to be visible in FIG. 22.

In young stems of *Pereskiopsis* and *Quiabentia*, the numerous, more or less closely aggregated druses of the hypodermal layer are compact and rotund (FIG. 20) and commonly differ from the diffusely distributed ones of the inner cortex which tend to be of stellate form (FIG. 21). During development of the crystalliferous hypodermis, enlargement of the crystals presses the epidermal cells outwardly and laterally, thus more or less drastically modifying their form and arrangement. Not infrequently the druses press laterally into the intercellular channels subtending the stomata and at least partly occlude their entrances.

Anatomically more specialized species of *Pereskia* exhibit less consistent differences in distinguishing the genus from *Pereskiopsis* and *Quiabentia*. In the case of *P. aculeata* Mill. and such Peruvian and Bolivian pereskias as *P. humboldtii* Britt. & Rose, *P. weberiana* Schum., and *P. diaz-romero-ana* Cárd. (which have markedly divergent trends of specialization in their xylem, Bailey, 1962, 1963a) there is a tendency for the outer cortical layers in young stems to become conspicuously thicker-walled and to appear at least pseudo-collenchymatous. Furthermore, although no typical crystalliferous hypodermis is formed, there is a tendency for relatively widely spaced, often linearly arranged aggregations of rotund druses to occur in the outermost layer of the cortex. Such occurrences are at least suggestive of possible initial trends of specialization which become exaggerated and dominant in *Pereskiopsis* and *Quiabentia*.

The stomata in normally developing leaves of these taxa have cuticular ledges resembling those of *Pereskia sacharosa* and allied taxa. However, young stems have consistently more numerous stomata than do those of the primitive category of pereskias. The lowermost internodes of the Andean pereskias prior to periderm formation tend to have a thick cuticle and massive intercellular accumulations of cutin intruding between the epidermal cells as in *P. sacharosa* and allied taxa, but they have more extensive deposits of cutin overlying the guard cells and accessory cells as in *Pereskiopsis* and *Quiabentia* (FIG. 13). In the case of *P. aculeata* periderm formation is so precocious in young shoots that I have not succeeded in obtaining internodes bearing stomata in stages of elongation and

increase in circumference comparable to those available in collections of the Andean pereskias. In younger developing internodes of *P. aculeata* the cuticle is thin and jackets a conspicuously papillose outer surface.

As shown in the first paper of this series (Bailey, 1960), *Pereskia pititache* Karw. (*P. conzattii* Britt. & Rose), *P. autumnalis* (Eichlam) Rose and *P. nicoyana* Web. differ from the pinnately veined pereskias in having palmate or pseudo-palmate venation comparable to that which occurs in *Pereskiopsis* and *Quiabentia*. However, the divergent trends of specialization in the xylem of these taxa are less advanced than in *P. aculeata* and the Andean pereskias (Bailey, 1963b). The cuticle overlying the epidermal cells may be smooth (FIG. 3) or it may have contraction folds, i.e., cuticular striations (FIG. 6) comparable to those that occur in other pereskias. The stomatal apparatuses in surface views of leaves vary markedly in form in the three taxa. In thick, fully expanded leaves from trees growing in the wild, the stomata differ from those of previously discussed categories of pereskias in having massive accumulations of cutin overlying the guard cells, as in *Pereskiopsis* and *Quiabentia*. Periderm formation is so precocious in young shoots of these pereskias that Dr. Boke and I have not succeeded as yet in obtaining material adequate for determining whether similar stomata occur in stems. However, since the cork cambium of cacti commonly arises by periclinal divisions in the epidermis, it is possible to observe after periderm formation is initiated that no collenchymatous layers or crystalliferous hypodermis are formed in young stems of the three pereskias.

In the case of *Pereskia colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose and *P. portulacifolia* Haw. adequate collections of roots and stems were obtained for studying divergent trends of specialization in the xylem (Bailey 1963d). Unfortunately only a few collections of leaves and young stems have been obtainable thus far. Available evidence at present suggests, however, that the stomatal apparatuses of these taxa not only have slender cuticular ledges, but also accumulations of cutin penetrating between the guard cells and subsidiary cells. These deposits of cutin are much less massive than those which occur in the preceding category of pereskias and in *Pereskiopsis* and *Quiabentia*. Stomata are of infrequent occurrence in the epidermis of young stems, thus resembling the situation in *P. sacharosa* and allied taxa, but the cuticles are thin and devoid of massive intercellular intrusions of the epidermis. The stems are devoid of collenchymatous layers and a crystalliferous hypodermis.

DISCUSSION AND CONCLUSIONS

In preceding papers of this series I have shown that *Pereskiopsis* and *Quiabentia* may be differentiated anatomically from *Pereskia* by (1) the characteristic development in young stems of a highly specialized crystalliferous hypodermis in these genera (Bailey, 1961b), by (2) the absence of diagnostic forms of sclereids in their secondary phloem (Bailey, 1961a),

and except in comparisons with *Pereskia pititache*, *P. autumnalis* and *P. nicoyana*, by (3) the characteristic palmate or pseudo-palmate vasculature of their leaves (Bailey, 1960). In addition, I have shown on preceding pages that, except in comparison with stems of *Pereskia aculeata* and the Andean pereskias, *Pereskiopsis* and *Quiabentia* are characterized by having typical collenchymatous outer cortical layers.

A preliminary investigation of cuticles, epidermal cells, and stomatal apparatuses reveals such wide ranges of variability within taxa, particularly in superficial views of stomatal apparatuses, as to be of questionable taxonomic reliability unless based upon very extensive collections of material from plants of different ages when grown under different environmental influences. However, detailed investigation of periclinal and anticlinal sections of available leaves and young stems reveals some structural differences of apparently potential taxonomic significance. The occurrence of punctate and reticulate structures in the outer periclinal walls of epidermal cells in leaves of *Pereskiopsis* and *Quiabentia* may eventually provide a useful criterion in differentiating the foliar appendages of these genera from those of *Pereskia*. Furthermore differences in thickness of the cuticle, in intercellular accumulations of cutin between cells of the epidermis, and in the deposition of cutin in the frontal cavity or vestibule of stomatal apparatuses have at least supplementary significance in differentiating certain categories of *Pereskia*, and in separating one or two of them from *Pereskiopsis* and *Quiabentia*.

It should be emphasized again in this connection that investigations of the cuticle, epidermis and stomatal apparatuses, and of the subtending outer cortical layers of young stems prior to periderm formation are particularly desirable from a physiological point of view, i.e., in regard to the functioning of stomata, and in retention of moisture in leaves and young stems of plants growing in semi-arid or arid environments.

In the case of *Pereskia sacharosa*, *P. grandifolia* and allied taxa, stomata frequently are few in number or absent on the upper surface of the relatively large thin leaves, and on the surfaces of internodes of young stems prior to periderm formation which tends to be more or less precocious in its development. The stomatal apparatuses, even on the under surfaces of the leaves, exhibit no conspicuous structural modifications for the prevention of water loss such as occur in many dicotyledons growing in arid environments. This may be due at least in part to the abscission of leaves at the end of a rainy season. Although the internodes of young stems prior to periderm formation have very thick cuticles and massive intercellular accumulations of cutin between the epidermal cells (which may have some physiological significance during the dry season), the cuticle overlying the stomatal apparatuses is tenuous, and there are no conspicuous structural adaptations for the prevention of loss of moisture. If the stomata are actually functional, as seems questionable in some cases, regulation of moisture probably is controlled merely by the opening and closing of the stomatal aperture.

In the case of *Pereskiopsis* and *Quiabentia* and such pereskias as *P.*

pititache and allied taxa, the massive accumulations of cutin in the stomatal apparatuses of fully matured leaves prior to abscission, and in the fully elongated internodes of young stems shortly prior to periderm formation raises important physiological questions regarding the functioning of stomata in these plants. In such stomatal apparatuses as those illustrated in Figs. 17 and 18 it appears unlikely that the stomata can be fully functional even where the guard cells contain vestiges of viable protoplasts. In certain of my collections the guard cells of some or all of the adjacent stomatal apparatuses have collapsed and are thoroughly impregnated with cutin (Fig. 9). It is of interest in this connection that some of the druses in fully matured cells of the crystalliferous hypodermis may be partly or completely jacketed by cutin.

In general in the leaf-bearing Cactaceae the ordinary epidermal cells appear to be devoid of chloroplasts, but where the stomata appear to be potentially functional with partly or fully open apertures, the guard cells, and sometimes the subsidiary cells are packed with green plastids (Fig. 8). This raises the question whether stomata which are functional during earlier stages of the development of leaves and young stems subsequently become occluded and incapable of functional activity as in Fig. 9. In some taxa the epidermis is in direct contact with subtending thin walled chlorenchymatous tissue, whereas in young stems of some taxa it is separated from such tissue by layers of thick walled collenchymatous cells. The collenchymatous tissue, like the epidermis, contains few if any chloroplasts and, since it is devoid of intercellular spaces, must retard the movement of gases and water vapor except in intercellular channels subtending the stomata.

It should be emphasized in conclusion that a preliminary investigation of the cuticle, epidermis, stomatal apparatuses, and subepidermal layers of the most primitive surviving representatives of the Cactaceae reveal salient trends of structural specialization whose functional significance can be fully and reliably elucidated only by sustained experimental and other observations on plants growing in their native habitats. Such detailed experimental investigations, in adequate correlation with anatomical and enviromental ones, are at present much needed for a clearer understanding of salient adaptations in the Cactaceae which are essential for survival in arid environments.

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EXPLANATION OF PLATES

PLATE I

Figs. 1–4. Epidermal layers of leaves, stained in Haidenhein's haematoxylin and sudan III and mounted in glycerin, × 200. 1, *Pereskia grandifolia* [*Castellanos*], epidermal layer from leaf preserved in F.A.A. 2, *Pereskiopsis scandens* [N.Y. Bot. Gard.], epidermal layer from leaf preserved in F.A.A. 3, *Pereskia pititache* [*Boke*], epidermal peel from small thin leaf of young elongating shoot of a greenhouse plant. 4, *Pereskiopsis* [*Boke* B–20], epidermal layer from leaf preserved in F.A.A.

PLATE II

Figs. 5–9. Cuticular striations and stomatal apparatuses. 5, *Pereskia sacharosa* [N.Y. Bot. Gard.], epidermal peel from leaf stained in sudan III showing radially and irregularly oriented cuticular striations, × 420. 6, *Pereskia pititache* [*Boke*], epidermal layer from large thick leaf of an old tree growing in the wild, stained in sudan III, showing convoluted forms of cuticular striations, × 330. 7, *Pereskia sacharosa* [N.Y. Bot. Gard.], anticlinal section of leaf stained in safranin and haematoxylin, showing stomatal apparatus and subtending intercellular cavity in the chlorenchymatous tissue, × 420. 8, *Pereskia grandifolia* [*Boke*], epidermal peel from leaf, stained in sudan III, showing chloroplasts in guard cells of stomata, × 510. 9, *Pereskia* aff. *humboldtii* [*Ferreyra*], epidermal layer from stem stained in sudan III, showing collapsed guard cells plugged with cutin, × 420.

PLATE III

Figs. 11–13. Epidermal layers of stems preserved in F.A.A., stained in sudan III and mounted in glycerin, × 260. 11, *Pereskia grandifolia* [*Castellanos*]. 12, *Pereskia* aff. *bleo* [*Rodriguez*]. 13, *Pereskiopsis scandens* [N.Y. Bot. Gard.].

PLATE IV

FIGS. 14–18. Sectional views of young stems prior to periderm formation. 14, *Pereskia tampicana* [*Boke*], stained in haematoxylin and safranin, showing cuticle, epidermis, and thin walled cells of mesophyll, × 200. 15, *Pereskia diaz-romeroana* [*Cárdenas*], stained in haematoxylin and safranin, showing cuticular ledges in frontal cavity or vestibule of stomatal apparatus, outer pseudo-collenchymatous layers of cortex appearing black, × 420. 16, *Pereskia grandifolia* [*Moran 7270*], cuticle stained intensely with sudan III and mounted in glycerin, × 420. 17, *Pereskiopsis aquosa* [N.Y. Bot. Gard.], cuticle stained with sudan III, showing massive accumulation of cutin in frontal cavity, overlying the guard cells and penetrating between the guard cells and the subsidiary cells, × 420. 18, *Pereskiopsis porteri* [N.Y. Bot. Gard.], cuticle stained with sudan III showing massive intercellular intrusions of cutin, depression of guard cells inwardly, and marked reduction in their diameter, × 420.
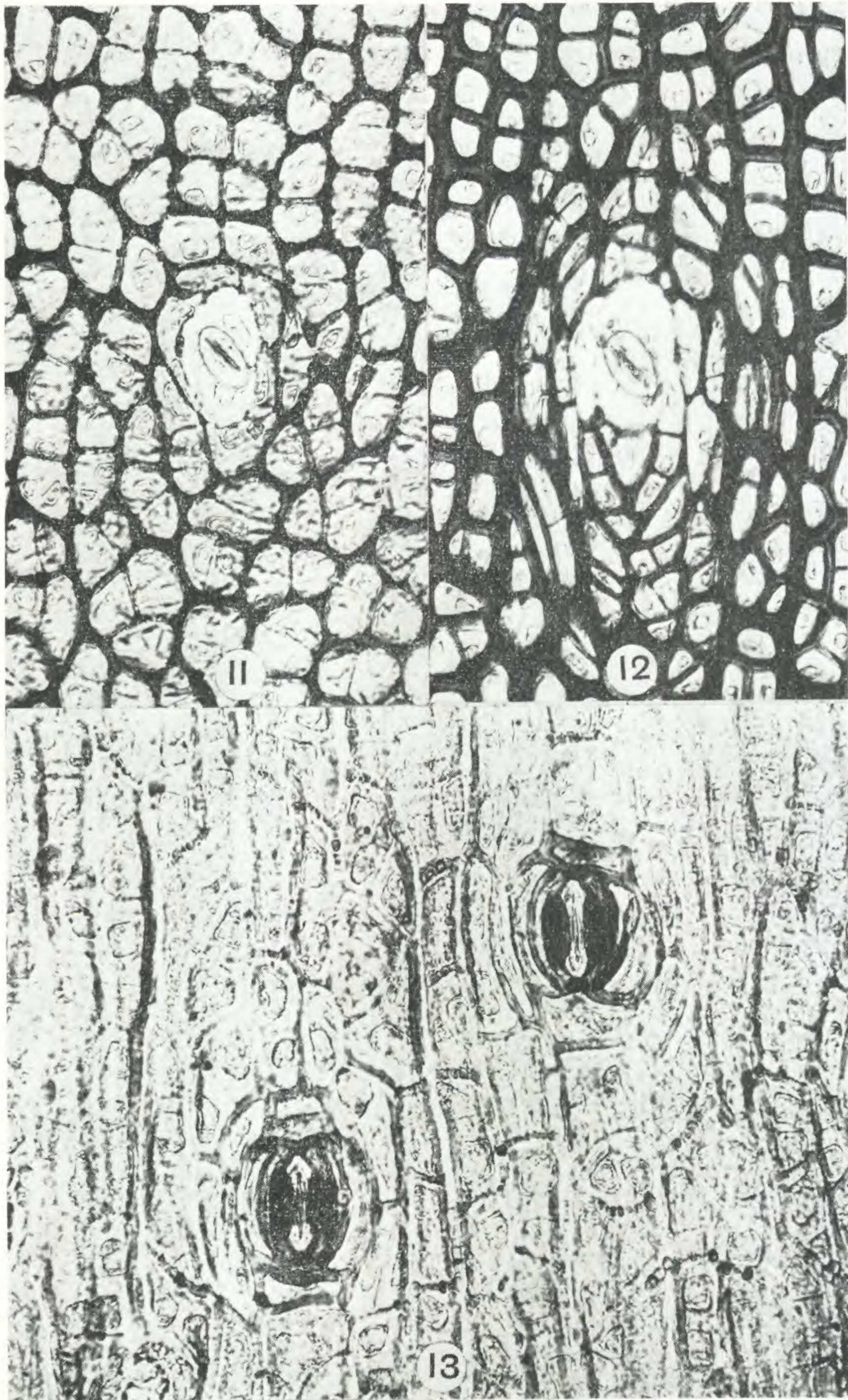
PLATE V

FIGS. 19–22. Details of collenchymatous and crystalliferous layers. 19, *Pereskiopsis scandens* [N.Y. Bot. Gard.], section of young stem stained in haematoxylin and safranin showing contrast in thickness of walls of the inner chlorenchymatous cortex and the outer collenchymatous layers which are devoid of intercellular spaces except in channels subtending the stomata, × 200. 20, *Pereskiopsis aquosa* [N.Y. Bot. Gard.], showing form of druse in crystalliferous hypodermis, × 510. 21, *The same*, showing form of druses in chlorenchymatous cortex, × 510. 22, *Pereskiopsis chapistle* [Mo. Bot. Gard.], tangential section of collenchymatous layers stained in haematoxylin, showing intercellular channel and character of primary wall "pitting," × 200.
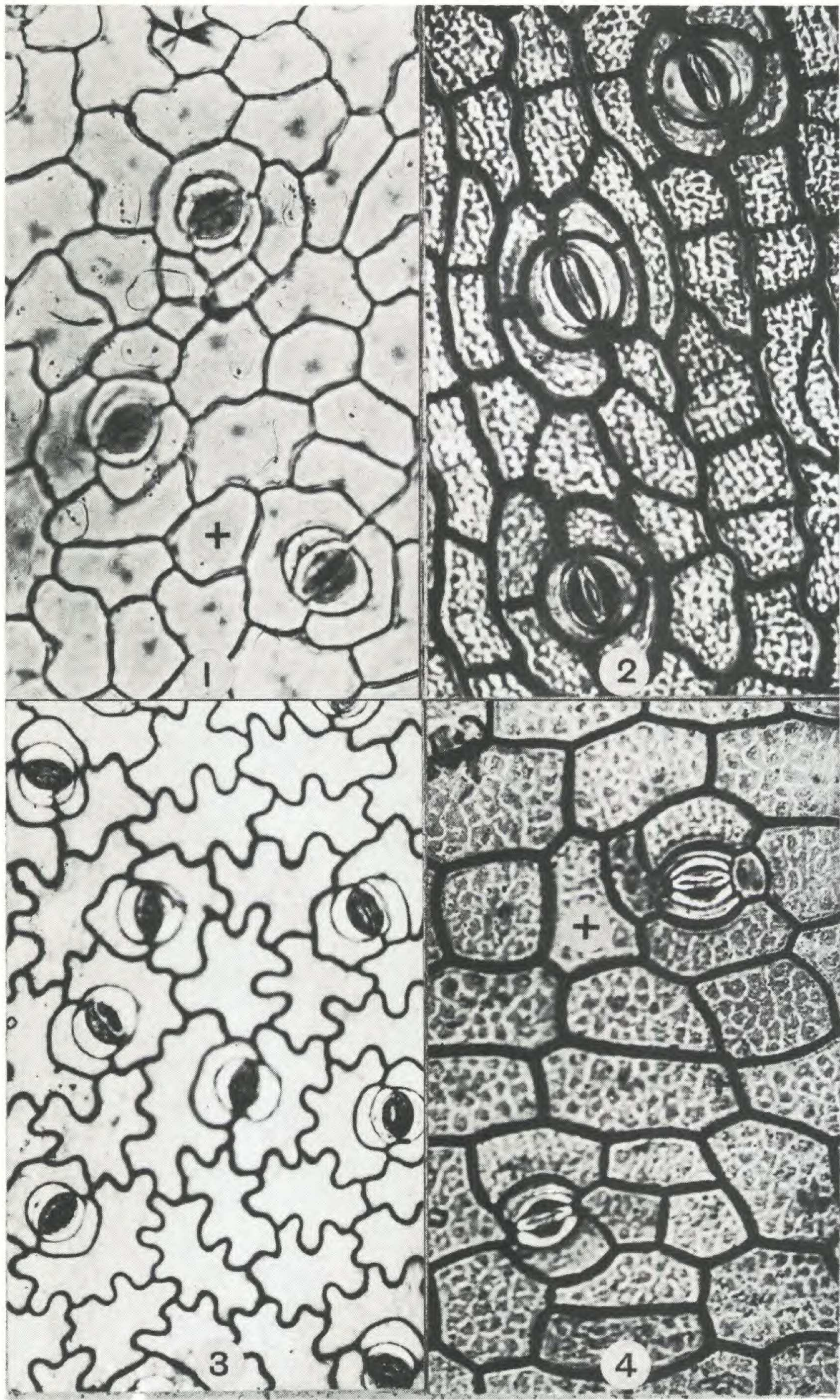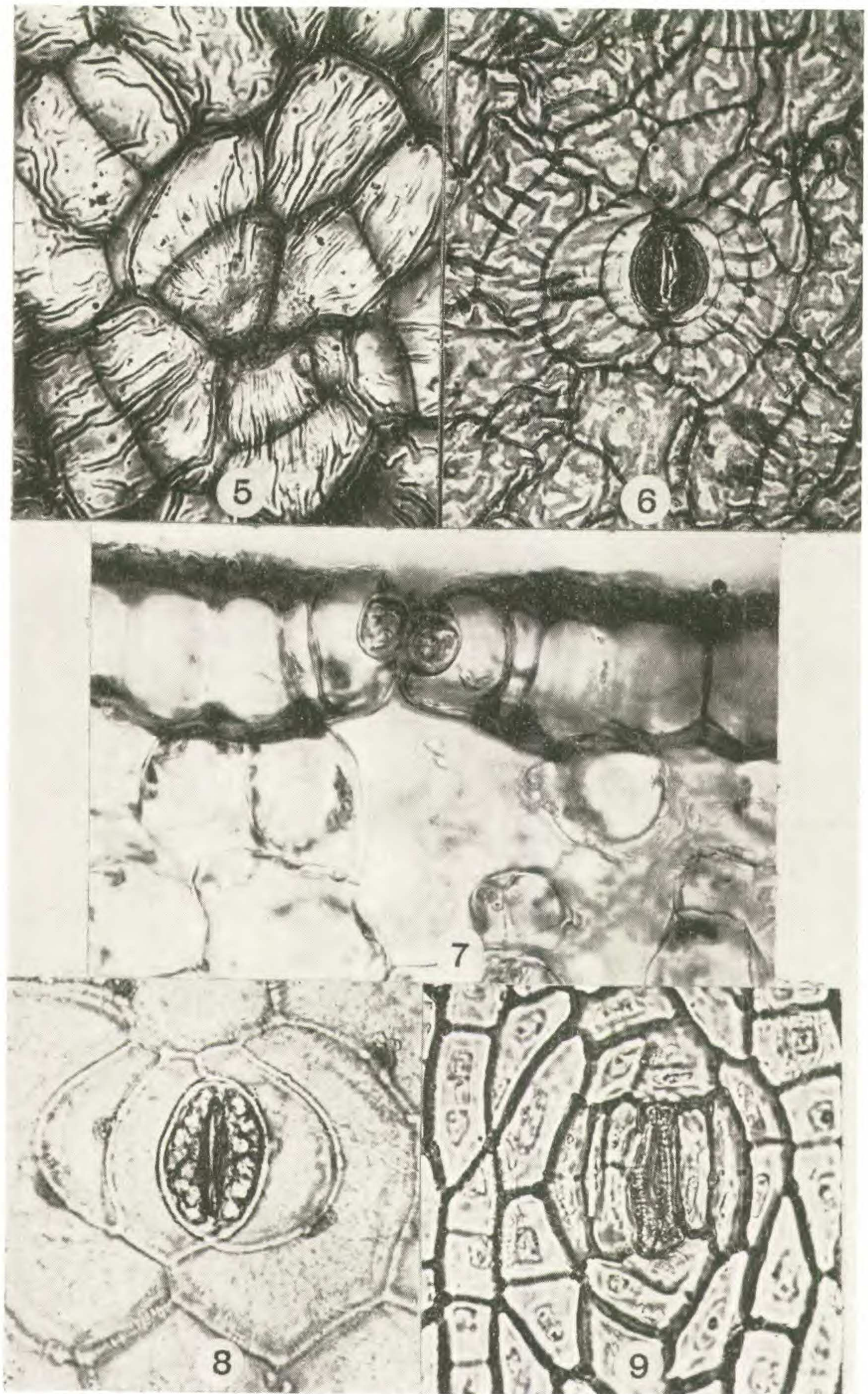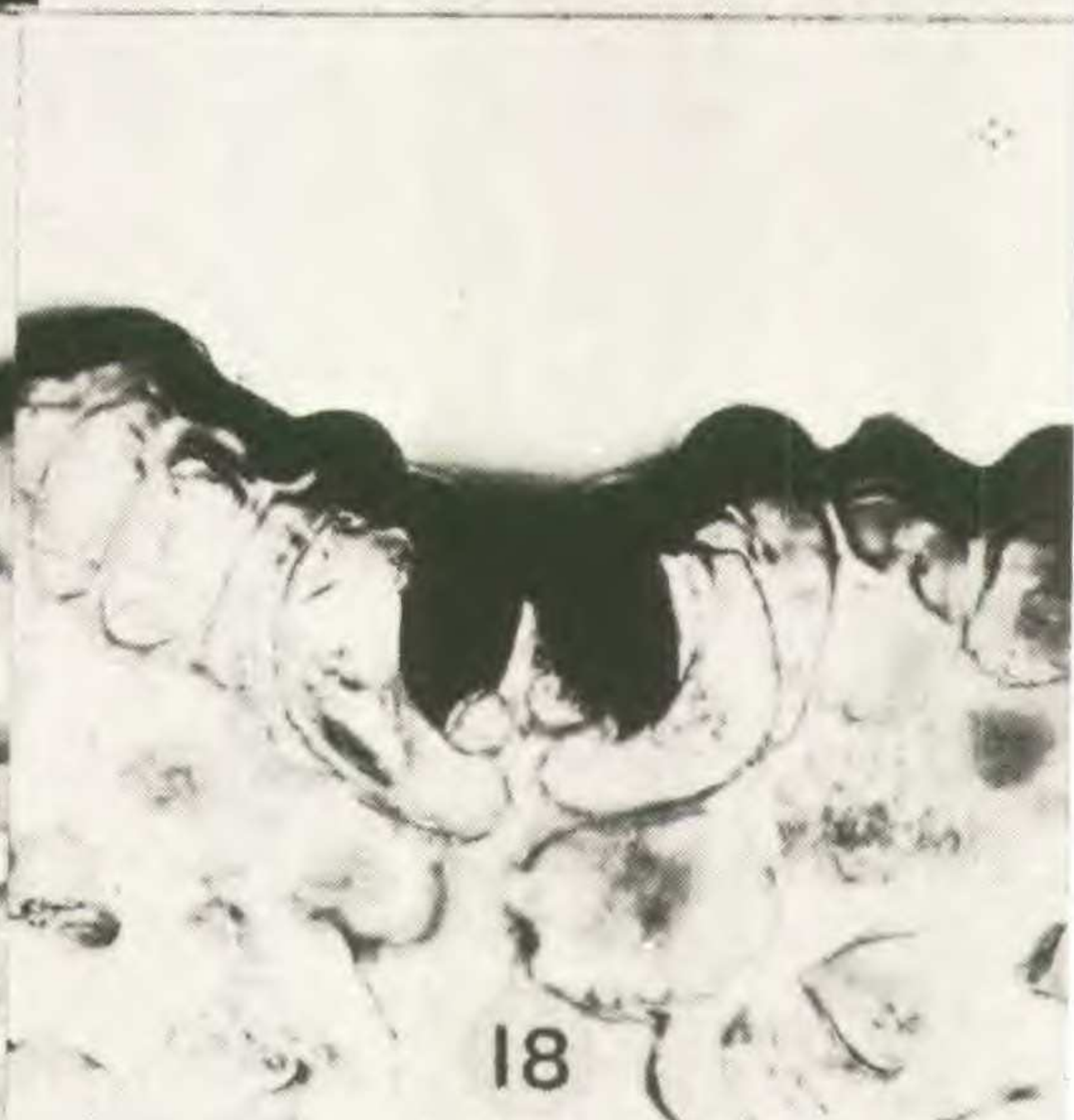
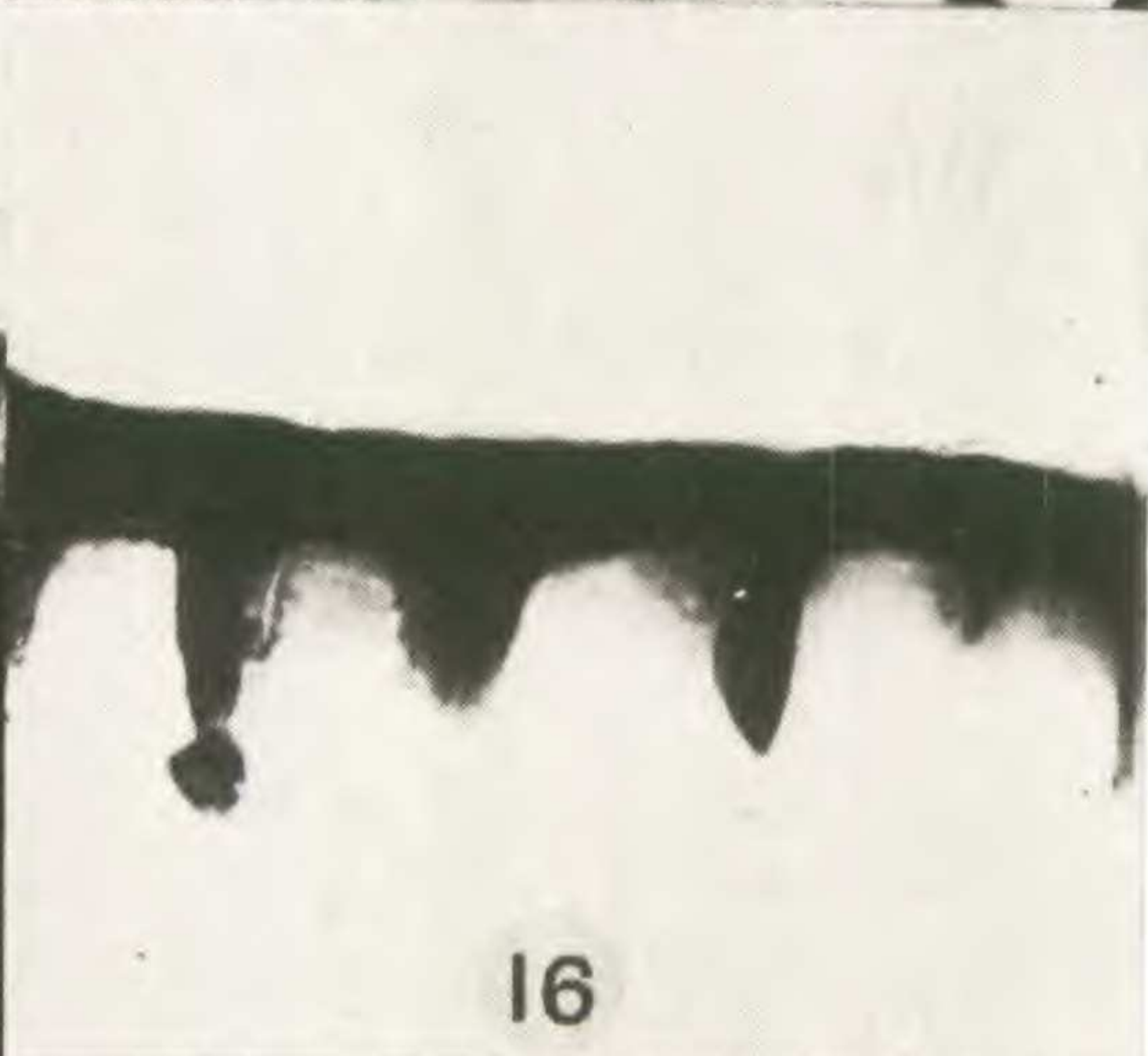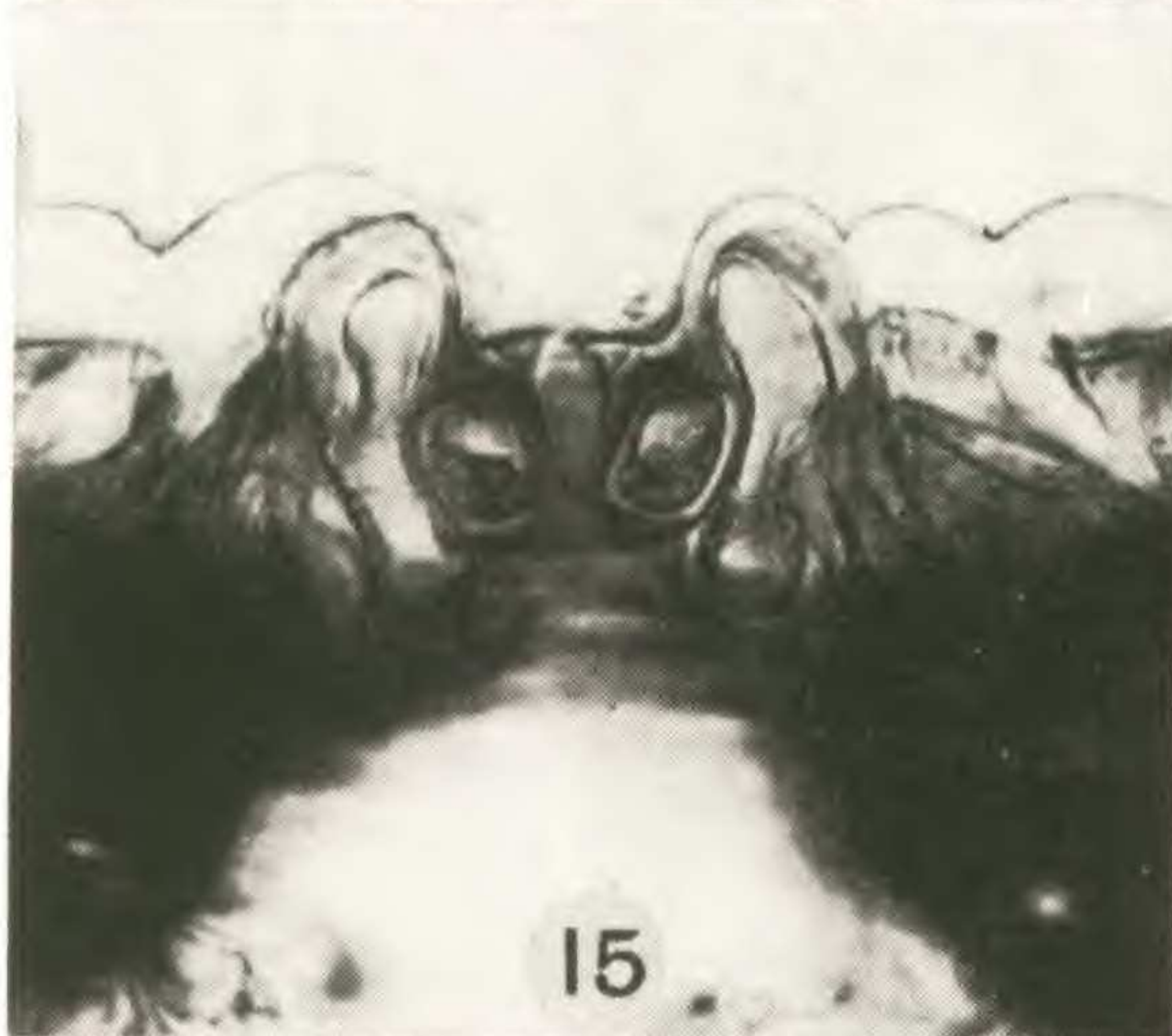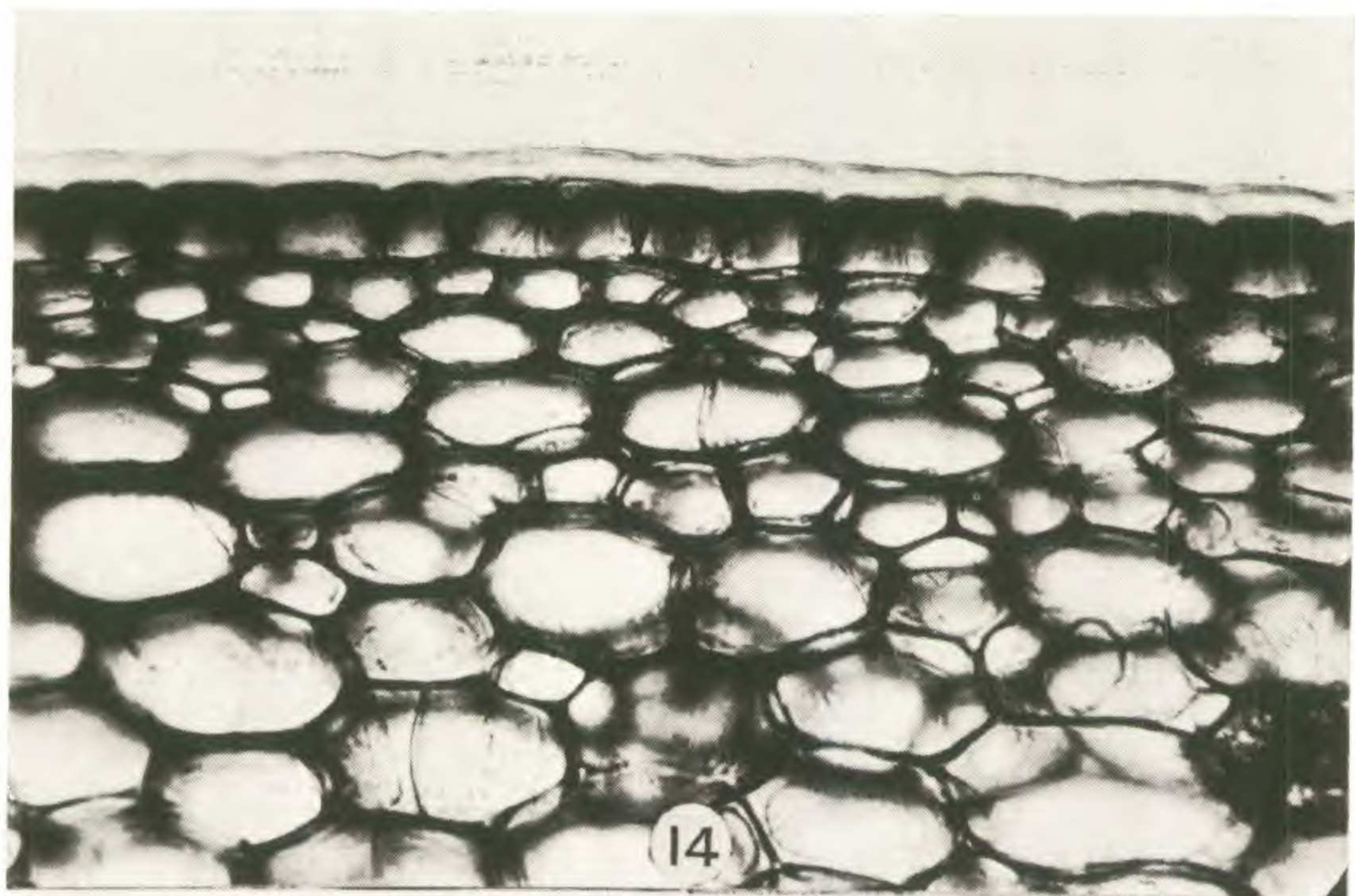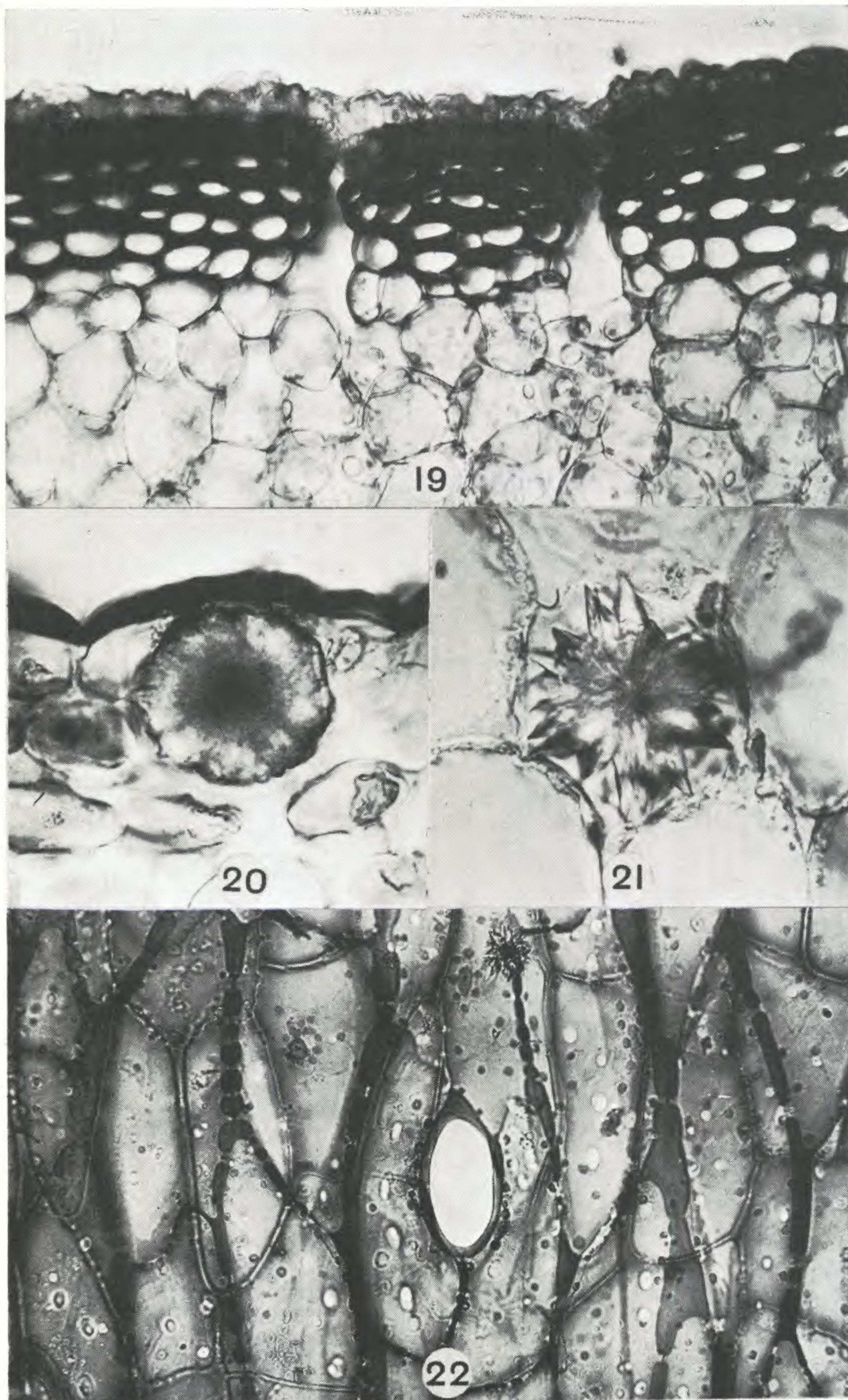BAILEY, LEAF-BEARING CACTACEAE, XII

Bailey, Leaf-bearing Cactaceae, XII

PLATE III

BAILEY, LEAF-BEARING CACTACEAE, XII